

CHAPTER 1: INTRODUCTION

This effort was directed at 3 primary goals: 1) to describe patterns of biological diversity in lotic and lentic riparian ecosystems within a topographic basin; 2) to elucidate the environmental features and associated processes potentially responsible for observed patterns; and 3) to provide information and interpretations useful in the conservation of biological diversity within the Lake Tahoe basin, as well as in other similar environments. This chapter identifies the concepts and theories used to frame the problem and the approach to it, and provides an overview of the topics that will be addressed in following chapters. Chapters 1 through 10 of this document, including all the lotic riparian work, are the dissertation work of Patricia Manley. The remaining 2 chapters, including all the lentic riparian work, represent work jointly conducted by Patricia Manley and Matthew Schlesinger.

THE NATURE OF BIOLOGICAL DIVERSITY

What is Biological Diversity?

Definition of Biological Diversity

Through most of the 1970's and early 1980's, the operational definition for biodiversity was limited to relatively simple statements such as "the variety within and among stands of vegetation" (Boyce and Cost 1978). However, the definition has expanded over time. Biological diversity includes all biota from bacteria, fungi, and protozoa to higher plants, insects, fish, birds, and mammals. A more recent definition of biodiversity given by the U. S. Office of Technology Assessment (1987) is "the variety and variability among living organisms and the ecological complexes in which they occur." The concept of biological diversity can be applied to a wide range of spatial and organizational scales, including genetic, species, community, and landscape (Wilson and Peter 1988, Noss 1990, Jensen et al. 1993).

Alpha and Beta Diversity

Whittaker (1972) partitioned the concept of diversity into 3 facets: alpha, beta and gamma diversity. Alpha diversity is the number of distinct taxa (e.g., species, genera, families) in a given location as defined by the researcher (Primack 1993). Alpha diversity is most often represented by species richness, and locations can vary from small 1 m² sample plots (Huston 1979) to large 250,000 ha landscapes (Harrison et al. 1992). Beta diversity is the degree to which species composition changes along an environmental gradient (Whittaker 1972). For example, beta diversity is high if the species composition of an assemblage changes at successively higher elevations up a mountain side, but is low if the same species occupy the entire mountain side. Gamma diversity is variously interpreted as either (1) the rate at which additional species are encountered as geographical replacements within a similar environmental condition (e.g., vegetation zones) in different localities, or (2) regional diversity determined by the sum total of species across many sample units. Whittaker (1972) saw gamma diversity as the sum of alpha and beta diversity. In practice these indices are expected to be highly correlated (Primack 1993). Since Whittaker's introduction of these terms, others have added complexity and variation to the categorization and interpretation of these types of diversity (e.g., Harrison et al. 1992, Cody 1993, Ohmann and Spies 1998, Rey Benayas et al. 1999). In the study of lotic riparian ecosystems, I look at both alpha and beta diversity, and gamma diversity is treated as regional diversity as

defined by the total number of taxa occurring across all sample sites. In the study of lentic riparian ecosystems, we look only at alpha diversity.

Rarity

Rare taxa are those having low abundance or small ranges (Gaston 1994). Reveal's (1981) statement expands on this definition, in that "... rarity is merely the current status of an extant organism which, by any combination of biological or physical factors, is restricted either in numbers or areas to a level that is demonstrably less than the majority of other organisms of comparable taxonomic entities." The characteristics that distinguish rare and common species were summarized by Gaston and Kunin (1997) into 8 groups of traits: breeding systems, reproductive investment, dispersal ability, homozygosity, competitive ability, resource usage, trophic status and body size. Other factors that have been shown or proposed to differ between rare and common species include predation pressure, numbers of competitors, and numbers of coexisting species (see Gaston and Kunin 1997). In general, rare species tend to have lower reproductive potential, have poorer dispersal capabilities, be more genetically impoverished, have an inferior competitive ability, be more specialized in resource use (and associated with rare resources), belong to higher trophic levels, and have larger body sizes (Gaston and Kunin 1997).

Ecological communities tend to consist of a few relatively common species and many rare ones (Williams 1943, MacArthur 1957, Preston 1948, 1962, May 1975, Ugland and Gray 1982). Much debate exists about what ecological interpretation might best explain this distributional pattern. The simplest and most parsimonious explanation is that since each species is rare in most of the places where it occurs and abundant in a few places, the distribution of abundance among species in a local assemblage might simply represent a random sample of abundance of the individual species (Brown 1995). Since each species is believed to occupy a unique niche (Grinnell 1917, Elton 1927, Gause 1934, Hutchinson 1957), rare species then constitute not only the bulk of diversity in terms of species richness, but also represent a substantial proportion of the diversity of life history characteristics and functional roles in ecosystems (e.g., Wardle et al. 1998).

Extirpation and extinction are the ultimate processes by which biological diversity is reduced. Although rarity is generally a poor predictor of extirpation or extinction, it is associated with a higher probability of extirpation and is commonly used as an indication of vulnerability to extirpation or extinction (e.g., Williams and Given 1981, Perring and Farrell 1983, IUCN 1984, 1988). Thus, the rare species in a given assemblage constitute a substantial contribution to the biological diversity of an area, and data on their composition and environmental correlates can provide insights into the factors influencing and vulnerabilities facing biological diversity (Gaston 1994).

By definition, rare species are infrequently encountered and therefore they can be readily underrepresented or their associations masked by more common species in assessments of patterns of richness. In the study of lotic riparian ecosystems, I identified species rarely encountered in the study area and analyzed their patterns of richness to elucidate their contributions to biological diversity.

Factors Influencing Biological Diversity

Current biological diversity is a result of a variety of environmental events and processes, including past evolutionary developments, biogeographic processes, extinctions, and current influences. Processes influencing diversity operate at different spatial and temporal scales (MacArthur 1969, Schluter and Ricklefs 1993, Tilman and Pacala 1993) (Fig. 1). Local diversity is constrained proximally by resource abundance, competition, predation, and disturbance, but it is

also influenced by larger temporal and spatial scale processes and events such as emigration, large-scale disturbances, and evolution (MacArthur 1969).

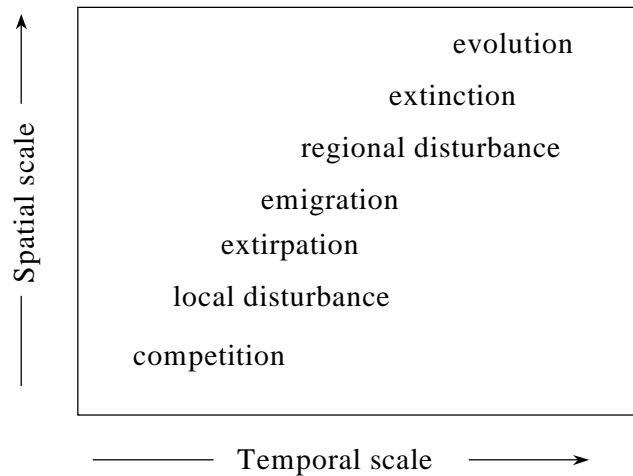


FIG. 1. The relative temporal and spatial scales of key ecological processes affecting biological diversity.

All the key processes identified in Figure 1 specifically contribute to observed diversity at landscape (e.g., basin) (Noss 1990) and larger scales. *Local disturbances* can include site specific, discrete disturbance events, such as tree falls, hikers or snowmobilers passing a given location, and small wildfires. *Competition and predation* are recognized as significant influences shaping species composition (e.g., Horn and MacArthur 1972, Pickett and White 1985, Tilman 1990). *Meso-scale disturbances* affect a large proportion of a basin of interest, and can be long-term, chronic, or permanent. These can include logging, human settlement, fire suppression, large wildfires, high tree mortality due to drought stress and insect infestation, road system. *Emigration* refers to the arrival of new species or recolonizations of species to a basin from another basin, and is also recognized as a major process shaping communities composition (e.g., Skellam 1951, Levin and Paine 1974). Basins are typically topographically isolated to some degree which will influence the rate and types of species that move into and out of a basin, including colonization and recolonization. *Extirpation* refers to the loss of a species occurrence. This can occur frequently because of the ubiquitous pressure of humans on species persistence. *Regional disturbance* refers to disturbances occurring at scales larger than a basin, such as climate changes, prolonged drought periods, large storms, air pollution from adjacent basins. *Extinction* occurs at a relatively slow rate, and except for local endemics, are a larger-scale phenomenon. Finally, *evolution* includes morphological and behavioral adaptations, as well as speciation. In this study, biological processes were not addressed directly, but rather abiotic and biotic correlates were used as surrogates for understanding processes most influencing patterns of biological diversity.

Patterns of Biological Diversity in Relation to Environmental Conditions

Alpha Diversity

A few driving environmental features have been shown to consistently influence diversity across a broad range of environments and spatial scales, namely productivity, which affects resource abundance, and spatial and temporal heterogeneity, which affects niche-space diversity (Vannote et al. 1980, Begon et al. 1990, Gregory et al. 1991, summary in Schluter and Ricklefs 1993). Patterns of biological diversity in relation to productivity and spatial heterogeneity are discussed below.

Productivity is the rate at which energy flows in an ecosystem (Rosenzweig 1995). The fundamental abiotic factors that affect productivity can also serve as ecological correlates for productivity, and they include elevation, precipitation, latitude, moisture availability, nutrients, and temperature (e.g., Pianka 1967, Brown and Davidson 1977). These largely abiotic factors affect all biota in some manner and can be treated as gradients along which relationships between productivity and diversity are assessed.

Biological diversity appears to have a complex relationship with productivity. Rosenzweig (1971) coined the term 'the paradox of enrichment' to describe the pattern observed in terrestrial systems where diversity is highest at intermediate levels of productivity. The explanation for this pattern is that when increased productivity results in an increased diversity of resources an increase in species richness is to be expected. However, above a certain point, increased productivity simply results in an increased supply of resources, providing a competitive advantage to species associated with the most abundant resources, and thereby reducing species richness. This pattern has been observed by many researchers for a variety of species groups and measures of productivity (Whittaker and Niering 1975, Huston 1979, Tilman 1982, Lonesdale 1988, Gradstein and Pocs 1989, also see Wright et al. 1993), however it is most appropriately applied and successfully observed in experiments conducted at small geographic scales where extraneous factors (most importantly disturbance) can be controlled. This pattern has not held for some investigations at larger geographic scales (e.g., Janzen et al. 1976, Terborgh 1977, Heaney and Rickart 1990), and while some investigators see these discrepancies as simply a matter of scale (i.e., only a portion of the productivity gradient was sampled), others see them as potential challenges to the theory.

In both the lotic and lentic work, the relationship of diversity to elevation, precipitation, and aspect, all of which relate strongly to productivity, was assessed. Productivity typically declines with increasing altitude in terrestrial environments because of the decline in both temperature and length of growing season (e.g., Pianka 1967). There is also generally a decrease in productivity with aridity, especially in relatively dry environments where water-supply may limit growth (e.g., Brown and Davidson 1977), and with decreased supply of essential nutrients like nitrogen, phosphorus, and potassium (Begon et al. 1990). In the northern hemisphere, south and west facing aspects tend to be drier and warmer than north and east facing aspects, and therefore can have various effects on productivity depending on whether moisture or temperature is more limiting.

Productivity clines also exist in aquatic environments. In stream systems, productivity generally increases from headwaters to mouth as the gradient of the stream declines, water flows more slowly, streams widen, floodplains widen, stream temperatures increase, riparian vegetation becomes more prevalent, and contributions of organic material into the stream increase. This increasing trend in stream productivity from headwaters to mouth is embodied in the concept of longitudinal succession and the river continuum concept (Vannote et al. 1980), which describes how physical changes in stream morphology from headwaters to mouth translate into changes in productivity, as expressed by nutrient availability and the composition and function of biological assemblages. In relation to stream-side environments, the increase in stream width, floodplain

width, and riparian vegetation are expected to have the greatest influence on biological diversity because together they increase moisture availability, as well as spatial heterogeneity. Numerous studies have shown an increase in alpha diversity with decreases in features such as gradient, floodplain width, and stream order (e.g., Sheldon 1968, Horwitz 1978, Vannote et al. 1980, Gregory et al. 1991).

Topographic and geomorphological features influence more than local microclimatic conditions and spatial heterogeneity, but also make an area less hospitable to species by affecting ease of movement, and in turn the intermixing of individuals through dispersal, extinction, and recolonization rates. Topographic or geomorphological impediments or barriers can result in reduced species richness (MacArthur and Wilson 1967).

Spatial heterogeneity, expressed as variation in vegetation structure, is an emergent property of the same abiotic factors affecting productivity. Thus, variations in vegetation structure can be treated as secondary biotic gradients along which relationships with diversity are assessed. Biological diversity is typically positively associated with spatial heterogeneity. Environments that are more spatially heterogeneous can be expected to accommodate a greater number of species because they provide a greater variety of microhabitats and microclimates (Cody 1975, Tonn and Magnuson 1982, Huston 1994, Rosenzweig 1995). For example, MacArthur and MacArthur (1961) formalized the relationship between the diversity of bird species and the complexity of vegetation, noting that the number of bird species in a habitat varies in direct proportion to the number of layers of vegetation. Similar relationships between alpha diversity and habitat complexity have been found in other taxonomic groups, such as lizards (Pianka 1967). In the lotic riparian work, I studied the relationship between biological diversity and vegetation structure to assess the potential influence of spatial heterogeneity on patterns of diversity.

Beta Diversity

Studies of species turnover along environmental gradients can provide important contributions to our understanding of the processes that affect species occurrence, and, in turn, greatly affect the biological diversity of a region. Gradient analysis was originally proposed as a mechanism to study shifts in plant species composition (Whittaker 1967), and has been used to study community concepts and beta diversity in plants (e.g., Shipley and Keddy 1987, Vazquez and Givnish 1998). The use of gradient analysis to address and describe processes potentially affecting species distributions can be applicable and useful for a wide variety of taxa, including birds, invertebrates, mammals, and reptiles (Terborgh 1971, Diamond 1973, Able and Noon 1976, Harrison 1992, Krasnov and Shenbrot 1998).

Shifts in species distributions are often studied along elevation gradients (e.g., Terborgh 1971, Able and Noon 1976, Vazquez and Givnish 1998), but a variety of other gradients have been explored, including floodplain connectivity (e.g., Tockner et al. 1999), disturbance (e.g., Rao et al. 1990, Rith 1998), moisture (e.g., Krasnov and Shenbrot 1998), and physical distance (e.g., Harrison et al. 1992). Most of these studies address one species group, such as birds, plants or invertebrates. Few studies have investigated beta diversity along multiple environmental gradients (e.g., Brockway 1998, Ohmann and Spies 1998).

Relationships between Alpha and Beta Diversity

The overall diversity of a given geographic area (gamma diversity) results from the contributions of both alpha and beta diversity. Alpha and beta diversity are driven by different ecological processes, and in a given geographic area they may have divergent associations with particular environmental factors. Alpha and beta diversity are often studied independently of one another, but a growing number of studies are attempting to address both sources of diversity in a given geographic area (e.g., Lapin and Barnes 1995, Dietrich and Scheidegger 1997, Rith 1998,

Zhang 1998, Tockner et al. 1999). Understanding the environmental factors that are responsible for observed alpha and beta diversity in an area provides valuable insights into the ecological processes most influencing each facet of diversity (alpha, beta, and gamma) and serves as a strong foundation for designing strategies to conserve biological diversity.

Variation Among Taxonomic Groups

Although theory predicts general patterns of diversity in relation to environmental factors, diversity should vary among species groups (e.g. birds, mammals, vascular plants) as a result of differences in basic life history strategies. Variations in mobility (sessile, walking, flying), thermoregulation (homeotherm vs. heterotherm), and trophic level (producer versus consumer) all contribute to expected differences in relationships between the diversity of taxonomic groups and environmental factors.

Most investigations of alpha or beta diversity have addressed only one taxonomic group. As discussed above, the processes that drive observed patterns of diversity have differential effects on species (and higher taxonomic levels) based on their life history traits. Two life history traits that have significant effects on variation in taxonomic richness are mobility and habitat specialization, some of the same factors identified as affecting rarity. Inferring process from pattern is facilitated by looking at a variety of taxonomic groups, as I did in the lotic riparian work, where the variation in their relationships to environmental features can help further elucidate the processes ultimately responsible for observed patterns of diversity.

Describing Biological Diversity

Ecosystems can be viewed as comprised of three distinct but related elements: components, structures, and processes (Noss 1990, Williams and Marcot 1991). Components are the kinds and amounts of plants, animals, soils, water, etc. Structure refers to spatial distribution or pattern (vertical or horizontal) of components. Processes refer to the flow or cycling of energy, materials, and nutrients through space and time.

This study focuses on patterns of composition and structure of species assemblages to better understand the past and present factors affecting biological diversity at the basin scale. This approach is aligned with the emerging field of macroecology (Brown 1995). Brown (1995) defined macroecology as, "...the way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution, and diversity." Macroecology emphasizes statistical pattern analysis rather than experimental manipulation as a mechanism for understanding and studying processes shaping populations and communities, and promotes this approach as complementary to a reductionist approach of studying individual interactions among species.

Biological diversity should be characterized with consideration of the dimensions in which it is expressed and the processes that affect it. In this study, I address four primary facets of biological diversity: alpha diversity, rarity, beta diversity, and gamma diversity. I treat alpha diversity as the richness or abundance of taxa at a given sample site, beta diversity as the shift in composition of taxa among sample sites along one or more gradients, and gamma diversity as the total richness within the basin resulting from the contributions of alpha and beta diversity. Analyzing patterns of rarity aids in the interpretation of observed patterns in alpha diversity.

Most researchers have applied descriptions of diversity to taxonomically similar species, such as fish, butterflies, or birds (Horwitz 1978, Debinski and Brussard 1994, Kremen 1994). However some researchers have looked across taxonomic groupings to better assess biological diversity in its entirety (e.g., Harrison et al. 1992, Krasnov and Shenbrot 1998, Tockner et al. 1999). The array of taxonomic assemblages serves to represent the range of responses to environmental

conditions that might be occurring across all biota. Analysis of multiple species groups in one study area should help differentiate true taxonomic differences in patterns of diversity from apparent differences that may result from looking across studies which may differ in scale and methods (Goerck 1997). In the lotic riparian work, I explored patterns of diversity within and among diverse taxonomic groups.

Environmental features can be described at a range of spatial scales and levels of resolution. Describing patterns of diversity in relation to environmental features requires that the scale and resolution at which environmental features are described be commensurate with descriptors of biological diversity. In studies of individual species, the ecological niche (Hutchinson 1957) of a species circumscribes the range of environmental conditions within which the species can exist, and points toward the relevant features of the environment that constitute its habitat (Morrison et al. 1992). In studies of the diversity of multiple taxa, a more generic approach must be taken to defining the geographic scales and characteristics of the environment that are relevant. In this study, macro-scale environmental features are identified as those that are not site specific, but rather were continuous gradients that operate over entire landscapes, such as elevation and climate. Meso-scale environmental features include basic, site-specific features such as aspect, gradient, channel morphometrics, and vegetation composition and structure. Micro-scale environmental features include high resolution features such as litter depth, microclimatic conditions, and chemical features. Micro-scale environmental features are most relevant when studying one or few similar taxa since relevant micro-scale features vary greatly among taxa.

TRENDS IN BIOLOGICAL DIVERSITY

Biological Diversity in California

The combination of the Mediterranean climate, rich geological history, complex topography, and diverse soils in California has produced a region of extraordinary biological richness (Jensen et al. 1993, Thelander and Crabtree 1994, Keeley and Swift 1995, Rundel 1998, Walter 1998). However, California is increasingly becoming known for its degraded natural resources, including toxic waste sites, the most polluted air basins in the nation, and the largest number of endangered species of any state in the continental US (Jensen et al. 1993). Alterations of the landscape are increasing as the population continues to grow (FRRAP 1988).

Statistics for California's biological diversity are consistent with global trends in biological diversity. Recent estimates of California's biological diversity enumerate 748 species of vertebrate animals, about 25,000 insects, almost 5,200 vascular plants, and 380 natural communities (Jones and Stokes Assoc. 1987). From 25 to 40 % of California's vertebrate taxa (varies by taxonomic group) have been determined to be formally listed as threatened, endangered or have the potential to be listed in the near future (Jones and Stokes Assoc. 1987). Data are lacking on invertebrates and non-vascular plants, but their populations are likely to have similar trends. Overall, California currently has one of the highest number of Federally Threatened and Endangered species of any state in the continental U. S.

Status of Riparian Ecosystems

Riparian ecosystems are an unusually diverse mosaic of landforms, communities, and environments with high biological diversity (Naiman et al. 1993). Riparian ecosystems are defined here as the interface between terrestrial and aquatic ecosystems (Gregory et al. 1991). Riparian ecosystems are some of the most productive and ecologically diverse ecosystems in California and the Sierra Nevada. For example, of the 401 species of mammals, birds, reptiles and

amphibians in the Sierra Nevada, approximately 21% depend on riparian environments (Graber 1996). The biological diversity of riparian environments results from a vicissitude of attributes, such as moisture availability, structural complexity, and microclimatic characteristics. However, riparian environments are one of the least researched ecosystems relative to their contribution to biological diversity (Kauffman 1988). Despite their importance, they are rarely mapped and, therefore, are commonly overlooked in land use planning exercises (Kondolf et al. 1996).

Riparian ecosystems are of widespread concern within California because they are becoming increasingly impacted by human populations. Landscape transformation and ecological degradation have reduced wetlands and riparian habitats to less than 10% of their spatial expanse in less than 100 years (Walter 1998). In the Sierra Nevada, riparian environments have been highly altered over the past 150 years as a result of gold mining, gravel mining, dams, agriculture, grazing, fire suppression, recreation, exotics, and urbanization (Kondolf et al. 1996). Activities most impacting the Lake Tahoe basin were gold mining (in Nevada leading to timber harvest in the basin), grazing, fire suppression, and urbanization (Elliott-Fisk et al. 1997). Although riparian environments are currently managed with the intent of protection and restoration (TRPA 1982, TRPA 1986a, USDA 1988), the effects of past activities combined with increasing urbanization and recreation use result in riparian conditions that are degraded or at risk of degradation.

Conservation of Biological Diversity

The conservation of biological diversity is now widely recognized among ecologists and land managers as of great importance (Soulé 1986, Wilson and Peter 1988), and has become a major issue for land management agencies and the public in California. In September 1991, over 30 state and federal agencies and local governments within the State of California created and signed a Memorandum of Understanding (MOU) entitled “California's Coordinated Regional Strategy to Conserve Biological Diversity.” This MOU signifies a recognition that biological diversity is of legitimate concern within the State. A recent scientific assessment of the status of ecosystems in the Lake Tahoe basin (Murphy and Knopp 2000) included an assessment of the status of biological integrity and diversity, reflecting the public's concern and interest in biological diversity in the basin.

The conservation of biological diversity is hindered by several challenges, including incomplete information on factors influencing biological diversity, and the ability of institutions to respond to the information in light of uncertainties, inefficiencies, and costs. Informational barriers to conservation in California and the Lake Tahoe basin include the composition of taxa and the environmental factors influencing their distribution and abundance. The design and effectiveness of various conservation strategies depend on our understanding of the environmental features supporting biological diversity, as well as the motivation and ability of institutions to implement strategies once they are developed. However, in spite of uncertainties, incomplete information, and institutional barriers, land managers are faced with the task of conserving biological diversity.

RESEARCH OBJECTIVES

As described in the beginning of this chapter, this effort was directed at 3 primary goals: 1) to describe patterns of biological diversity in lotic and lentic riparian ecosystems within a topographic basin; 2) to elucidate the environmental features and underlying processes potentially responsible for observed patterns; and 3) to provide information and interpretations useful in the conservation of biological diversity within the Lake Tahoe basin, as well as in other similar environments. Three primary questions were addressed in this study.

1. What are the primary environmental conditions and gradients within the study area?
2. What are the relationships of various facets of biological diversity (alpha diversity, rarity, and beta diversity in lotic riparian ecosystems; alpha diversity alone in lentic riparian ecosystems) with environmental conditions, gradients, and associated processes?
3. What implications do these relationships have for land management and the conservation of riparian biological diversity?

Lake Tahoe Basin

The study area was located in the Lake Tahoe basin, which occupies upper elevations and is dominated by upper montane and subalpine zones and mountain streams (see Chapter 2). The basin is generally confined to the lower end of the productivity continuum because it is confined to upper elevations (Fig. 2). As such, I would expect to find a positive relationship between alpha diversity (expressed as richness or abundance) and features associated with productivity, namely elevation, precipitation, and channel flow characteristics. Deviations from this pattern could be the result of confounding environmental features, such as topography, temperature, microclimates, spatial heterogeneity, or disturbance.

The Lake Tahoe basin is a unique and discrete physical feature within the Sierra Nevada mountain range. The steep elevational gradient of the basin, combined with its location in a transition area between coastal climate to the west and a continental climate to the east, creates a diverse set of macro and micro climates for a subalpine basin its size. This diversity is likely to translate into a diversity of biological characteristics, including the types and distributions of vegetation communities and plant and animal species. The colliding climatic regimes have created distinct biogeographic regions that meet in the basin, and may have created an elevated floral and faunal heterogeneity in the basin. In contrast, the large proportion of the basin occupied by Lake Tahoe (over 75%) serves to distribute what might be considered suitable conditions for terrestrial species of plants and animals in a relatively linear manner around the lake, and for riparian species along many, short, small order watersheds. Finally, the topographic features surrounding and creating the basin serve to create a bounded study area that can be described and studied as a discrete entity. These features make the Lake Tahoe basin an excellent geographic location for investigating the influence of ecological processes on biological diversity.

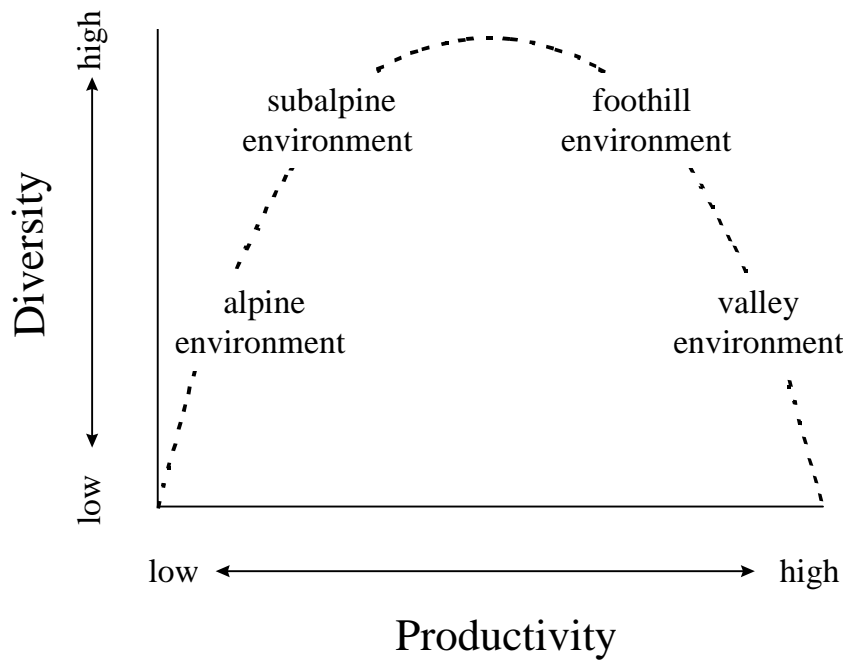


FIG. 2. Schematic of relationship between productivity and diversity.

Taxonomic Groups Studied

In this study, we addressed a total of 6 major taxonomic groups, 5 in lotic riparian ecosystems (birds, mammals, invertebrates, vascular plants, and macrofungi) and 3 in lentic riparian ecosystems (birds, amphibians, and littoral zone plants). One genus of snake was also assessed. Assemblages are defined here as phylogenetically related groups of species occurring at the same place at the same time (Fauth et al. 1996). These major taxonomic assemblages vary greatly in their life history traits, including mobility (amount and mechanism), thermoregulatory strategies, body size, and longevity. Many features also vary within these taxonomic groups, including prey, body size, and trophic level.

The selection of the 5 taxonomic groups for the lotic riparian work was based on a desire to represent as broad an array of taxa as possible in the study area, given the logistical constraints of the project. Birds and mammals are readily sampled, and are estimated to constitute an ecologically significant component of the biotic assemblage because they span a wide range of trophic levels and habitat associations. They vary greatly in their environmental associations and levels of specialization, and they are all relatively mobile. Amphibians and reptiles are more difficult to sample in the basin, particularly given their low numbers and relatively high habitat specialization. Amphibians and reptiles were detected, but only incidentally and thus were not included in the analysis of diversity. Invertebrates constitute a substantial proportion of animal biomass, as well as the majority of the animal diversity in the study area. Many invertebrates are also readily sampled, although sampling a significant proportion invertebrate richness is challenging. Because of their great diversity, invertebrates span a wide range of environmental conditions, ecological functions, and trophic levels. Vascular plants are estimated to constitute the majority of plant biomass in the study area, and also represent great diversity in their number, life forms, and environmental associations. Vascular plants are readily sampled, and their trophic role as producers provides a valuable contrast to the vertebrate and invertebrate species groups that

constitute consumers. Finally, fungi constitute a lesser known but fundamentally important biotic life form. Macrofungi were included in the study to broaden the taxonomic diversity and representation by the inclusion of a third kingdom, and because of the unusual and vital role they play in ecosystem function through nutrient cycling (Ascaso et al. 1982, Hudson 1986).

The selection of the 3 taxonomic groups for the lentic riparian work was based on the desire to address the majority of vertebrates species directly and address species primarily dependent on lentic ecosystems. Many aquatic feeding and nesting birds are primarily associated with lotic ecosystems in the basin. Amphibians are far more frequent and abundant in association with lentic habitats compared to lotic habitats in the basin. Plants occupying the littoral zone of lentic ecosystems may be vastly different from those in lotic ecosystems.

ORIENTATION TO THE CHAPTERS

This introductory chapter is followed by 11 chapters addressing a variety of topics. Chapter 2 describes the study area. Chapters 3 through 10 address various features and taxonomic groups associated with lotic riparian ecosystems. Chapter 3 describes methods for the lotic riparian work and an analysis of inter-year variation to determine if data could be pooled from 2 sample years into a seamless multi-year data set describing biological diversity. Annual variation was not a key feature of the study, but data collection spanned 2 years. The results of this analysis of inter-year variation was used to determine how to analyze the full data set such that inter-year variation did not contribute to misleading interpretations of patterns of biological diversity.

Chapters 4 through 10 present results and discussion on each of 7 topic areas. Chapter 4 addresses the environmental characteristics associated with lotic riparian ecosystems of the Lake Tahoe basin and establishes the foundation for describing environmental features in relation to patterns of diversity in lotic riparian ecosystems. The ensuing 5 chapters address each of the 5 taxonomic groups, in taxonomic order (with the exception of fungi): birds (Chapter 5), mammals (Chapter 6), invertebrates (Chapter 7), vascular plants (Chapter 8), and macrofungi (Chapter 9). Chapter 10 addresses patterns of diversity across the 5 taxonomic groups, and what these patterns suggest in terms of effective strategies for the conservation of biological diversity in lotic riparian ecosystems.

Chapter 11 addresses the environmental characteristics associated with lentic riparian ecosystems of the Lake Tahoe basin, and their associated diversity of birds, amphibians, and littoral zone plants. The final chapter, Chapter 12, addresses the environmental correlates of individual species of particular interest in association with lotic and lentic riparian ecosystems in the basin.